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AN ORGANISM PRODUCED SEXUALLY WITHOUT CHARACTERISTICS OF THE MOTHER.

By Th. Boveri.

[In offering a translation of Dr. Th. Boveri's paper, entitled Ein geschlechtlich erzeugter Organismus ohne mütterliche Eigenschaften, I have been guided by two motives. First, to make this paper, which will certainly become a classic in Biological literature, accessible to American students, since the journal in which it appeared "Sitz. d. Gesellschaft für Morphologie und Physiologie zur München" × Sitzung am 16 Juli, 1889, has a very limited circulation in this country.

In the second place, to point out the new avenues of research that such work opens. Results of this kind are of the utmost importance, inasmuch as they touch the very heart of the question of Heredity. Each advance in our knowledge gained by experimental work of this sort, carries forward rapidly our understanding of the most vital phenomena of life.

Results of this importance must be verified over and over again, until all chances of error (by no means small) are eliminated. Dr. Boveri writes that during the present Winter it is his hope to carry forward this work at Naples.

Three small wood cuts were given in the original paper. Dr. Boveri has most generously placed at my disposal the original drawings as well as five additional figures. These are added to the present account. The original figures gave side views of the Echinus larva, the Sphærechinus larva, and the side view of the bastard larva (Echinus ♂, Sphærechinus ♀). Three of the new figures give posterior views of the same larvæ and two of the *Dwarf Larvæ.*

Weismann, referring to Boveri's work, in his essay on Amphimixis affirms that *two spermatozoa enter the enucleated* egg to form the segmentation nucleus. I wish to call attention to the foot note in Boveri's paper, where it is positively stated that only *a single spermatozoon enters the enucleated egg.*

T. H. Morgan.]

Although the law, that the substances giving the definite and hereditary characters to the cell are entirely contained in the nucleus, is at times spoken of as a very probable hypothesis, but again even as a fact, yet it may be easily shown that this can be known to us neither in the well known phenomenon of fertilization of the egg, nor through the researches already carried out, concerning the rôle of the nucleus in the protozoa.

Simple reflection shows moreover that the determination whether or not this Theory of Inheritance (Vererbungs-Theorie) is true, can be settled in one way alone, viz., to take two different sorts of cells, utilizing the nucleus of one and the protoplasm of the other, to form a new cell. If the nucleus and protoplasm are so constituted that they can exist together, then will the properties arising from this cell, made artificially, answer our question. For then either the exclusive qualities of that cell will develop which had held the nucleus, or those will arise that come from the protoplasm, or lastly, from a mixture of both; showing whether the nucleus alone or the protoplasm alone (or both of the two constituents) is able to transfer to the other the properties it possesses on account of its origin, so as to bring about a reverse result in the other.

The idea of inheritance in the narrower sense corresponds to such a choice of the two cells, that the cell produced artificially out of the nucleus of the one and the protoplasm of another forms a cell capable of development.

Moreover in the case of the egg, as in no other, an opportunity is given to solve the question; because for no other cell do we possess so accurate a method of judging of its qualities as is given in the egg by means of the adult organism that comes from the egg.

Rauber[1] has already carried on a research of this sort. He describes it as follows. " The nucleus of the first segmentation sphere of a frog's egg was drawn out an hour after fertilization, by means of a pipette stuck into it. The same process was carried out in a fertilized toad's egg. These two pipettes were exchanged, and the nucleus of the toad's egg placed in the frog's egg, and the nucleus of the frog's egg into the toad's egg. Now if the nucleus alone carries the hereditary functions then there must develop out of the frog's egg a toad, and out of the toad's egg a frog." As was to be anticipated, the eggs did not develop further, and at first sight there seems to be no reason to expect that such an experiment should succeed. For if we were in a position to take out, without further injury, the nucleus from cells, still we could scarcely introduce by artificial means a new nucleus, without causing such fundamental alterations of the one or the other part, as to make further life impossible.

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[1] Rauber Zoologischer Auzeiger 15 March, 1886, pp. 17–.

But just here Nature herself offers the solution by means of which we can accomplish our purpose, because it makes the second and more difficult part of the experiment an entirely normal process—the entrance of the spermatozoon into the egg may be utilized.

The basis for my research is founded on the discovery of the Hertwig brothers.[2] When these investigators shook for a long time the eggs of the sea-urchin in a test tube, containing a small amount of water, in order to alter them mechanically, they found that in consequence of the shaking some of the eggs fell into pieces, and while some of the pieces contained nuclei, others did not. It was further shown that these enucleated (non-nucleated) fragments, as well as the nucleated ones could be fertilized, and that an active segmentative process took place in them. What followed in these cell masses was not determined by the Hertwigs. I have myself verified this discovery during my last visit to the Zoological station of Naples, and found *that the enucleated and fertilized fragments of eggs developed as far as and formed as complete larvæ as did the perfect nucleated* egg. From the enucleated fragments which I isolated I reared in a series of dishes larvæ[3] (about half of them developing normally) that formed *dwarf-larvæ.* These were in some cases only one-fourth as large as the normal larvæ, but otherwise agreed perfectly with these, and even lived for the same length of time, i. e., about seven days.

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[2] O. and R. Hertwig. Ueber den Befruchtungs und Theilungs-Vorgang des Thierischen Eies unter dem Einfluss ausserer Agentien Jena 1887.

[3] In a more extended account of my experiments I will describe in detail the methods which must be used in order to be certain that we are dealing with pieces without nuclei, and on the other hand the best method to give the more delicate pieces favorable conditions of development. Here I may remark that in order to obtain positive results, a sufficient size of the fragment is necessary, also that they have a nearly spherical form and sufficient amount of water for their development, and that MONOSPHERIC FERTILIZATION TAKES PLACE.

This result is in itself certainly full of interest. It shows that the sperm-nucleus itself possesses all of the properties necessary to function as the first segmentation nucleus, and the result, which shows the prevailing opinion concerning the nature of fertilization to be erroneous, gives an important support to my view, published in several places, concerning the interpretation of the process. I desist from considering the point further here, in order to turn to the interpretation of the experiments dealing with the questions raised concerning inheritance.

With the possibility of fertilizing enucleated egg-pieces and of bringing these to a normal development, we have fulfilled all of the conditions in order to reach the end which Rauber failed to attain. We have an enucleated egg—for the fragment has the value of an entire egg, and we are able by means of a process of fertilization to introduce another nucleus into the egg, the egg still possessing the power to develop. And now instead of using a spermatozoon of the same species, we introduce the spermatozoon of another in order to produce the hypothetical case of "the toad's egg and the frog's nucleus."

It is even possible to bastardise the egg fragments (obtained by shaking) of one species of sea-urchin with the sperm of another species, and to rear them far enough to determine whether the developing organism shows the qualities of both species or only of the one species. For such an experiment the sea-urchin presents favorable conditions. It is possible, although the results are somewhat variable, to cross-fertilize two species standing quite far apart. And in the second place the larva of the sea-urchin shows in a very few days, principally through the development of the calcareous skeleton, a very well defined shape. This is constant for each species and so well defined for each species, that at the age of four days we can distinguish the two species of larvæ just as easily and surely as in the adult condition.

The two species that I have used in my research are *Echinus microtuberculatus* and *Sphærechinus granularis.* I am certain that a more favorable combination than this can be found, for although the two species are well adapted inasmuch as their larvæ differ very considerably from one another, yet there is to be taken into account, the fact that cross-fertilization between the two is so difficult that in my experiment out of 1000 picked eggs (Sphærechinus ♀, Echinus ♂) not a single fertilized egg resulted. Of the four species found at Naples in great abund-

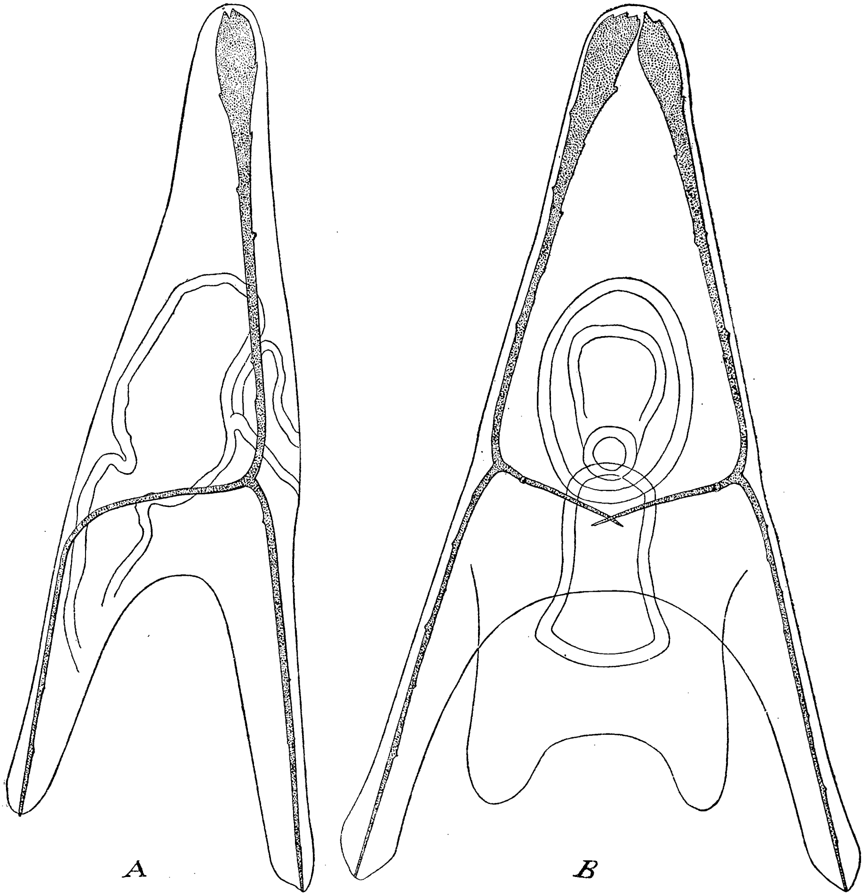

Fig. 1. *Echinus microtuberculatus* larva; pure type.

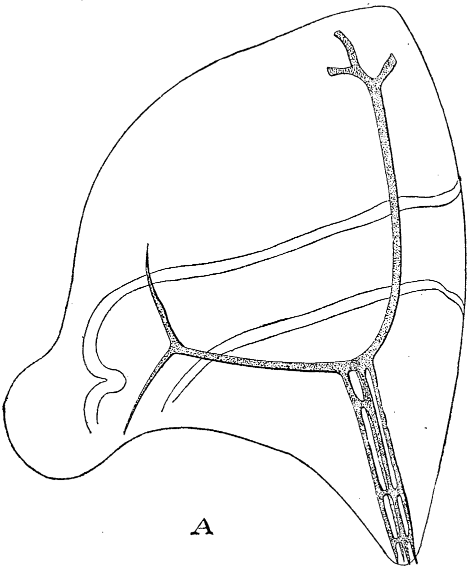

Fig. 2. *Sphærechinus granulatus* larva; pure type.

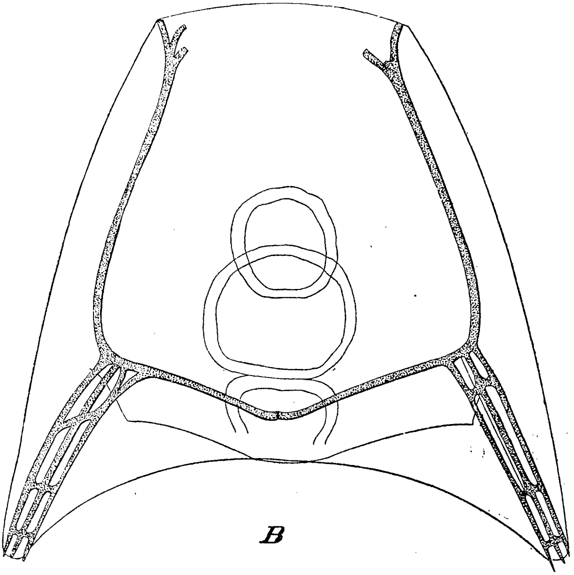

Fig. 2. *Sphærechinus granulatus* larva; pure type.

ance, these two alone are useful, and lend themselves to the solution of our problem.

Since the differences throughout are dependent on the distinctive peculiarities of the larvæ used, it is necesssry first to make clear the difference in structure of the larval forms that we are considering. The two accompanying figures will render a long account needless.

Fig. 1, A and B, represents an Echinus larva, and fig. 2, A and B, that of Sphærechinus. The two figures oriented alike, show the circumference of the body and the calcareous skeleton seen in profile [and in front]. The differences in structure of the body, particularly in the sheltered structures, are brought in these figures in the position best suited to the observer. The arrangement is sufficiently well shown in the figures to obviate any further description.[4] The enucleated egg-fragments of Sphærechinus were brought together with the sperm of Echinus.

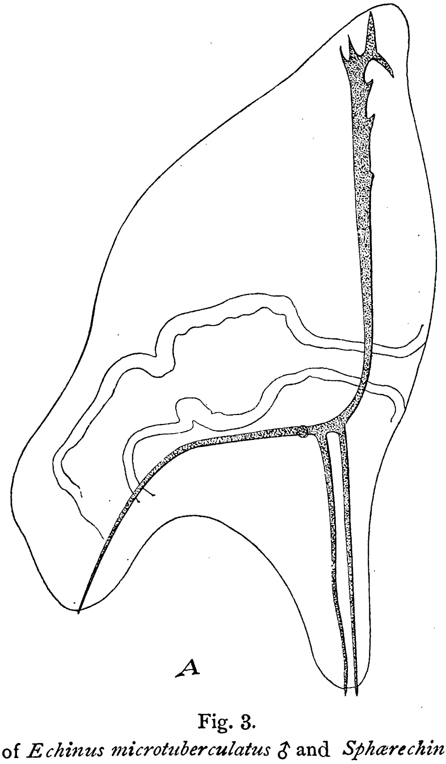

Fig. 3.
Larva of bastard of *Echinus microtuberculatus* ♂ and *Sphærechinus granularis* ♀.

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[4] The generic name will suffice, from this on, in speaking of these two species.

If the nuclear substance alone is the bearer of the parental qualities, then larva of the pure Echinus type will be produced (Fig. 1). It is clear that in the experiment this conclusion can only be proved, if the bastards produced from fertilized eggs (we will call these the genuine Bastard larvæ) give a middle-form standing between the larvæ of the two parental species. For it is conceivable that the particular structures of the two species might not be able to commingle, so that the larvæ would, according to their surroundings, develop either the paternal or maternal qualities alone (the qualities of the other parent in each case remaining latent). In this case there would be no true bastard.

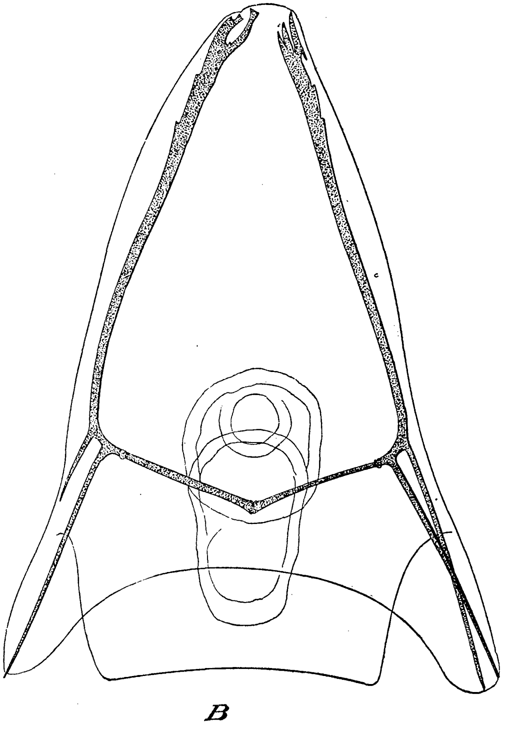

Fig. 3.

Larva of bastard of *Echinus microtuberculatus* ♂ and *Sphærechinus granularis* ♀.

I have reared such larvæ in great numbers and from many different individuals, and have in all certainly seen more than a thousand of them. The result was always the same. All genuine bastards, with not a single exception, represent both in the shape of the body as well as in the skeleton an almost exact middle form standing between the two parents. This is a new well defined form, and is always as such to be recognized and cannot be confused with either of the two parent larval forms. Fig. 3, A and B, which shows such a genuine Bastard larva, illustrates, as compared with figs. 1 and 2, this law better than many words could possibly do.

The result is otherwise if we shake into pieces the Sphærechinus egg before the entrance of the Echinus-spermatozoon. Certain of the eggs remain intact after the process, and these do give the genuine bastard form (Fig. 3). These are those formed from nucleated pieces, but another portion of the crossed larvæ agree entirely with the simple larva derived from the egg and spermatozoon of *Echinus microtuberculatus* (Fig. 1). These must have been produced chiefly from enucleated fragments. (Fig. 4 A and B.)

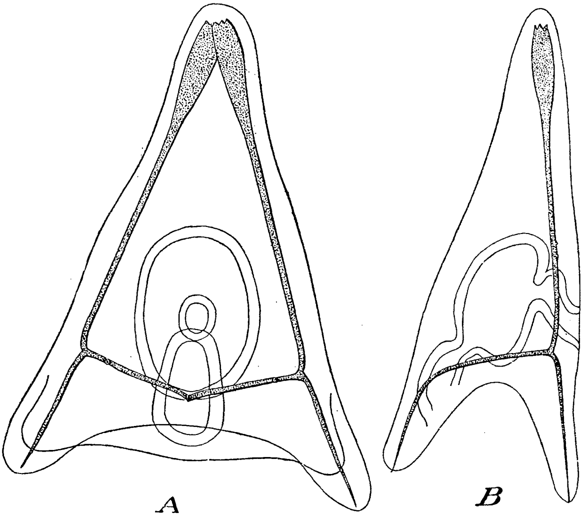

Fig. 4. Dwarf bastard larva of *Echinus* ♂ and *Sphærechinus* ♀ (fragment) of pure *Echinus* type.

That this is the correct interpretation is more clearly demonstrated by rearing in isolation the enucleated pieces. My results in this direction are on the whole not successful, and the explanation for this is to be found in the circumstance cited above, i. e., that the cross-fertilization between *Echinus microtuberculatus* ♂ and *Sphærechinus granularis* ♀ were scarcely ever successful out of 1000 cases. This small percentage of the whole number fertilized, where many millions of eggs or egg-fragments may be used, lends great improbability to the chance of getting successful results by isolating a few chosen examples of eggs. It is such a long and tiresome procedure to pick out and isolate the enucleated fragments from the shaken mass that in the limited time of my stay at the sea-shore I did not have the good fortune to see them develop in a single example.

I hold as sufficiently strong proof, in absence of direct knowledge, the result of those experiments in bastardization where enucleated were mingled with nucleated fragments, and with entire eggs. For after I have been able to reach the conclusion on the one hand by observing eggs and spermatozoa of the same species that enucleated pieces still develop, and on the other hand after it has been shown that the fertilization of nucleated eggs of Sphærechinus with Echinus sperm larvæ occasionally arise standing between the parent forms, there remains no other interpretation as to the origin of the dwarf-larva of pure Echinus except out of the enucleated fragments found there. But there remains a more definite result pointing to the correctness of such a conclusion. One can distinguish in a preserved and colored larva whether or not it has originated from a nucleated or enucleated egg, and this from the size of its nuclei. If the fertilized enucleated egg-fragment was the first segmentation nucleus which is formed entirely from A SPERMATOZOON NUCLEUS, the nucleus is half as large as a normal first segmentation nucleus, and this difference in size is handed down to all of the descendants of the egg cell, even to the larval stage. If now we kill larvæ of the same age derived from Sphærechinus eggs and egg-fragments fertilized by Echinus sperm, we have mixed together with the Bastard-type the true Echinus type, and the latter (true Echinus type) shows proportionately considerably smaller nuclei than the preceding one.

All doubt is thus removed, and it may be regarded as conclusive that by bastard fertilization of whole eggs or protoplasmic pieces having nuclei, larvæ are formed that stand midway between the larval forms of the parent species; but the larvæ arising from the *enucleated* fragments of eggs have entirely the characteristics of the parent (*male*) species. Herewith is demonstrated the law that the nucleus alone is the bearer of hereditary qualities. With the removal of the maternal nucleus are removed at the same time the maternal hereditary tendencies of the egg. And the maternal protoplasm, although in this case furnishing a large share of the material for the development of the new organism, is without influence on the form of the organism.

The phenomenon of growth of the enucleated protoplasmic mass is entirely governed by the introduced spermatozoon, and indeed to conclude by analogy, by the nucleus of the sperm. Whether the spermatic nucleus penetrates the egg protoplasm of its own species or of another species, the same result appears, namely, the larva is that of the male species. I might say that the nucleus possesses an assimilating power toward the protoplasm, since it produces the same sort of organism from material that appears to be different, according to our standards of truth. That the egg-protoplasm is similar in the two cases in every respect pertaining to its chemical constitution, I cannot admit, and do not even hold to be probable. Still such differences may, if they were present, be very easily explained, as due to the previous action of that nucleus, to which the enucleated protoplasm was at one time united, and any difference would thus not be incompatible with the law that all changes of form of the protoplasm are dependent on the constitution of the nucleus.